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# OFFSPRING SEX AND DURATION OF POST-FLEDGING PARENTAL CARE IN THE SEXUALLY SIZE DIMORPHIC NAZCA BOOBY (*SULA GRANTI*)

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**Resumen. – El sexo de las crías no influencia la duración del cuidado parental en volantones del Piquero de Nazca (*Sula granti*), una especie dimórfica en tamaño. –** En especies de tamaño dimórfico, generalmente el sexo de mayor tamaño requiere más alimento que el más pequeño, pero los padres usualmente no satisfacen las necesidades de sus crías más grandes. Aquí analizamos la presencia en el nido de los padres y las crías de Piquero de Nazca (*Sula granti*, un ave marina en la cual la hembra es más grande), durante el periodo cuando las crías pueden volar, pero aun retornan al nido para recibir alimento. Evaluamos la hipótesis nula de que el cuidado parental no difiere durante este periodo entre crías machos y hembras, complementando datos anteriores durante el periodo previo a ser volantones. Usamos las patrones de presencia para inferir la duración del cuidado parental de madres y padres por separado, con relación al sexo de la cría. No encontramos diferencias en la duración de la asociación entre padres y crías durante este periodo, ni en el crecimiento de éstas, lo cual tampoco se relacionó con su sexo. El cuidado parental aparentemente termina cuando la cría deja la colonia. El número de días en que los padres visitaron su nido durante el periodo posterior a que sus crías se tornen volantones no tuvo diferencias según el sexo de la cría. Nuestros resultados indican un cuidado parental similar para crías machos o hembras durante este periodo, a pesar de que las hembras requieren más cuidado que los machos para alcanzar el mismo nivel de condición física.

**Abstract. –** The larger sex in sexually size dimorphic bird species generally requires more food than the smaller sex does, but parents often fail to meet the needs of their larger offspring. Here we analyze nest attendance of Nazca Booby (*Sula granti*, a seabird with female-larger sexual size dimorphism) parents and offspring during the period of mobile dependence, when offspring can fly but still attend the nest to receive meals. We tested the null hypothesis that parental care to male and female offspring during this period does not differ, complementing previous data on the pre-fledging period. We used attendance to infer the duration of parental care by mothers and fathers, separately, with respect to offspring sex. The duration of the parental association with their offspring during this period, and offspring growth, did not differ by offspring sex, and parental care apparently ended when offspring vacated the natal colony. The number of days parents were observed at their nest site during the post-fledging dependency period did not differ by offspring sex. Our results indicate similar parental care for male and female offspring during the post-fledging dependency period, despite female offspring probably requiring more care than males to reach the same level of condition. *Accepted 23 May 2011*.

**Key words:** Nazca Booby, *Sula granti*, post-fledging parental care, sex-specific parental effort, sexual size dimorphism.

## INTRODUCTION

Parental care in nidicolous birds has been studied extensively during the period in which offspring are confined to the nest. Offspring of many species, including seabirds, continue to receive parental care after becoming sufficiently mobile to spend time away from the nest (Burger 1980, Arroyo et al. 2002, Wheelwright & Templeton 2003). This period of mobile dependence could involve daytime hours away from the nest and returning to the nest occasionally to meet parents for food, gathering in crèches away from the natal nest, or permanent nest-leaving with one or both parents. During this period of mobile dependence, young birds learn crucial life skills and often have a high risk of mortality (Burger 1980, Marchetti & Price 1989, Wheelwright & Templeton 2003). Some aspects of parental care of mobile offspring, such as "brood division", where one parent provides most of the care for one or more fledglings, are well documented in passerines (Wheelwright *et al.* 2003). Many nidicolous seabirds also exhibit some form of extended post-fledging parental care (Burger 1980, Nelson 1983). Recent studies have pointed to the importance of this rarely examined life history stage (Ricklefs 2010) by suggesting that increased parental investment during the post-fledging period in tropical species may explain differences in clutch size between tropical and temperate birds (Styrsky *et al.* 2005, Ricklefs 2010, Robinson *et al.* 2010). Yet this important developmental period and critical component of avian parental care remains poorly understood because observations of the family can be difficult when offspring are no longer confined to the nest.

Here we focus on parental care during the period of mobile dependence in which male and female offspring probably differ in food requirement. A review of studies of nestling bird food requirements indicated that the degree of sexual size dimorphism reliably predicted disparity in sex-specific food requirements, but that parents often failed to meet the excess requirements of the larger sex (Townsend *et al.* 2007). Previously, we examined parental effort during the nestling stage in the female-larger (Nelson 1978, Apanius *et al.* 2008) Nazca Booby (*Sula granti*; Family Sulidae), a predatory tropical seabird, and found similar levels of parental care provided to male and female offspring (Townsend *et al.* 2007), despite the fact that female nestlings are larger than are male nestlings (Townsend *et al.* 2007, Apanius *et al.* 2008). Nazca Boobies are long-lived (Anderson & Apanius 2003) with a low reproductive rate, raising only a single offspring per year (Humphries *et al.* 2006).

Townsend *et al.* (2007) investigated parental effort in Nazca Boobies from egg hatching to the "1% down" developmental stage, when 99% of the nestling's down has been replaced by pennaceous juvenile plumage and growth is nearly complete. Nazca Booby parents continue to feed their nest-based young from the 1% down stage until they leave the colony as juveniles several weeks later (Nelson 1978). Little mortality occurs from the 1% down stage until colony-leaving in this species (Humphries *et al.* 2006, Maness *et al.* 2007). Male and female offspring might receive different amounts of parental care during this period, which has not been studied to this point.

We tested the null hypothesis that parental care to male and female offspring does not differ after the 1% down stage by analyzing nest attendance (number of days present during the observation period) of Nazca Booby parents and offspring between fledging (taking flight for the first time) and permanent nest-leaving. Our objectives were to determine: (1) if one offspring sex received more care during this period than the other and (2) if the duration of post-fledging period differed by offspring sex. We used nest attendance patterns to infer the duration of parental care by male and female parents, separately, with respect to offspring sex. Our results extend our understanding of sex-specific parental care (Anderson & Ricklefs 1992, Townsend *et al.* 2007, Apanius *et al.* 2008) by offspring sex to the end of the period of offspring dependence for the first time in a sulid (Table 1).

## METHODS

*Study area.* We studied a population of Nazca Boobies at Punta Cevallos, Isla Española, Galápagos Islands (01°23'S, 89°37'W), Ecuador. The study site comprises three subcolonies, detailed in Huyvaert & Anderson (2004) and Apanius *et al.* (2008). Our group began banding adults and offspring in this population in 1984 as part of a long-term demographic study (Huyvaert & Anderson 2004, Apanius *et al.* 2008). All nests in the study site with at least one banded parent were monitored daily beginning in the 1992–93 breeding season (Apanius *et al.* 2008) from the date of clutch initiation until nestlings attained juvenile plumage or the reproductive attempt failed. Most nests with two unbanded parents were "unmonitored" unless the nest was located within a subsection of Subcolony 1 known as the "Study Area" (Apanius *et al.* 2008). In most years, all young that attain juvenile plumage were marked with a permanent uniquely numbered steel leg band regardless of monitoring status.

*Field procedures.* Volant offspring in juvenile plumage ("fledglings") leave the nest for increasingly longer periods of time each day, making determination of the actual date of permanent nest-leaving difficult. All young in the colony that attained juvenile plumage during the 1998–99 breeding season were marked with an additional uniquely numbered aluminum band augmented with small numbers painted on the breast to monitor presence of young boobies at their nest sites. Numbers on the bands and breast were easily visible from a distance of several meters. We searched the entire colony for double-banded fledglings at least twice daily (morning and evening) to ascertain when young flew to sea for the first time, inferred by observation of clean feet (feet of non-volant young are covered with excrement), and when young left the colony permanently (= last observation). Fledglings and parents in the "Study Area" in 2001–02 only (instead of the whole colony as in 1998–99) were given uniquely numbered, colored plastic bands (green = fledglings, gray = mothers, black = fathers) to examine nest and colony attendance patterns of parents and their offspring. Numbers on these additional bands were also large and easily read from a distance. We searched the Study Area twice daily (morning and late evening) for offspring and parents and searched the entire colony after dark with headlamps each night for plastic-banded birds. Most birds leave the colony in the morning and return in the late afternoon and evening and peak feeding time occurs between 14:30 h and 18:30 h (Anderson & Ricklefs 1992, Townsend *et al.* 2007, Maness & Anderson 2008) but do not necessarily attend their nest sites when in the colony. Nest visits and colony searches were timed to maximize the probability of observing banded parents and their young. We calculated the dates of the first flight to sea (hereafter "first flight") and the last observation of offspring, and attendance patterns of male and female parents from these data. Offspring that died after reaching the 1% down stage (a developmental stage when 99% of the nestling's down has been replaced by pennaceous juvenile plumage and growth is nearly complete; Humphries *et al.* 2006), but before leaving the island, were omitted from all analyses.

TABLE 1. Duration of the period of dependence after nest-leaving in the Sulidae. *Morus* spp. do not have a post-fledging care period ("n.a." = not applicable). *This is the standard deviation range around the mean; other numbers in this table are range of observed feedings.

| Species | Duration of parental care after nest-leaving (days) | Duration differs by offspring sex | Differential parental attendance by offspring sex | Reference |
|---|---|---|---|---|
| Abbott's Booby (*Papasula abbotti*) | 162–260 | ? | ? | Nelson & Powell 1986 |
| Northern Gannet (*Morus bassana*) | 0 | n.a. | n.a. | Nelson 1978; Mowbray 2002 |
| Cape Gannet (*Morus capensis*) | 0 | n.a. | n.a. | Jarvis 1974 |
| Australasian Gannet (*Morus serrator*) | 0 | n.a. | n.a. | Nelson 1978 |
| Red-footed Booby | 90–180 | ? | ? | Diamond 1974 |
| (*Sula sula*) | 28–90 | ? | ? | Nelson 1978 |
| | 108–128* | ? | ? | Guo *et al.* 2010 |
| Brown Booby | 42–259 | ? | ? | Simmons 1967 |
| (*Sula leucogaster*) | 42–119 | ? | ? | Nelson 1978 |
| | 21–56 | ? | ? | Schreiber & Norton 2002 |
| Blue-footed Booby (*Sula nebouxii*) | 28–42 | ? | ? | Nelson 1978 |
| Peruvian Booby (*Sula variegata*) | 28–60 | ? | ? | Nelson 1978 |
| Masked Booby (*Sula dactylatra*) | 21–28 | ? | ? | Nelson 1978 |
| Nazca Booby | 30–62 | ? | ? | Nelson 1978 |
| (*Sula granti*) | 35–55* | no | no | this study |

Our study included 127 families (72 male and 55 female offspring) in 1998–99 and 50 families (25 male and 25 female offspring) in 2001–02. Both 1998–99 and 2001–02 were below-average years for reproductive success at our study site (Maness *et al.* 2007) and the fledging sex ratio was significantly male-biased in 1998–99 (0.586; 95% CI = 0.532–0.639) but not in 2001–02 (0.517; 95% CI = 0.478–0.557; unpubl. data), suggesting that daughters might have been more difficult for parents to rear in 1998–99. Female Nazca Boobies are larger than males as adults and as nestlings (Townsend *et al.* 2007, Apanius *et al.* 2008), suggesting that young females might require more food provisioning and suffer higher mortality risk during food shortages than do young males (Anderson *et al.* 1993, Cameron-Macmillan *et al.* 2007). We looked for sex differences in developmental schedules between three developmental timepoints (the 1% down stage to first flight, and first flight to last observation). We examined parental nest attendance patterns during the second period only, because our attendance data from the 1% down stage to first flight to sea are incomplete.

*Sex identification.* Male and female adults can be distinguished by vocal pitch (Nelson 1978), but dependent young cannot be sexed by morphology or vocal pitch. We collected feather samples from all fledglings in 1998–99 and blood samples from nestlings in 2001–02 for molecular sexing. Feathers were preserved dry in plastic bags. Blood samples were collected by brachial venipuncture onto a filter paper tab, and preserved in 70% EtOH. We followed a modified PCR protocol of Fridolfsson & Ellegren (1999). Details of DNA extraction, the PCR protocol, and validation of the technique are provided in Maness *et al.* (2007) and Apanius *et al.* (2008). This technique was 100% accurate for this species Maness *et al.* (2007).

*Morphological measurements.* All nestlings were weighed (g) and their culmen and flattened wing cord lengths (mm) were measured on the day they reached the 1% down stage. We continued measuring offspring in 1998–99 until offspring were last observed in the colony. We collected data systematically between the 1% down stage and first flight in 2001–02 only. We used these measurements to track changes in morphological measurements between the 1% down stage and first flight, and between first flight and last observation, monitoring changes in size as a function of sex. We could not predict when an offspring would take its first flight or when it would leave the colony permanently and measurements were rarely taken on the day of first flight and not on the day of colony departure. Thus, we used the closest measurement taken before the day in question. Offspring not measured between two developmental stages (e.g., 1% down and first flight) were omitted. Changes in body mass and in culmen and wing lengths were analyzed separately by sex with years combined.

*Statistical analyses.* We used t-tests with separate variance estimates to compare the durations of post-fledging colony attendance of male and female offspring, and to compare the durations of the post-fledging period across the two years of this study. The age at which offspring reach developmental landmarks such as the 1% down stage, first flight, and last observation is variable; therefore, we used ANCOVA to compare of the number of days parents were present at their nest site using number of days between developmental stages as the covariate. We made three different comparisons of days present during post-fledging dependence to evaluate the effect of offspring sex on the number of days parents were present at their nest site: male parents of male offspring vs male parents of female offspring, female parents of male offspring vs female parents of female offspring, and both parents of male offspring vs both parents of female offspring (since parents could coordinate visits to their nest). To evaluate the effect of offspring sex on within-pair dynamics, we used a repeated measures ANCOVA test to determine if mates (fathers vs mothers) attended their shared nest differently by offspring sex during the post-fledging period.

Wilcoxon matched pair tests were used to determine if parents were present at the nest more before or after their offspring departed the colony to assess the possibility that parents and offspring vacated the colony together. We also examined the probability of parental presence at the nest site during the weeks before and after their offspring was last observed using mark-recapture model selection implemented in Program MARK (White & Burnham 1999). Candidate models included survival (S) probability and resight (p) probability parameters. Survival probability was fixed at one because all parents survived the two week period examined. Resight probability could remain constant (.) or vary by offspring sex (sex), or year (t). We used Akaike's Information Criterion (AIC) for model selection and ranking (Burnham & Anderson 2002). In practice, we used QAICc,

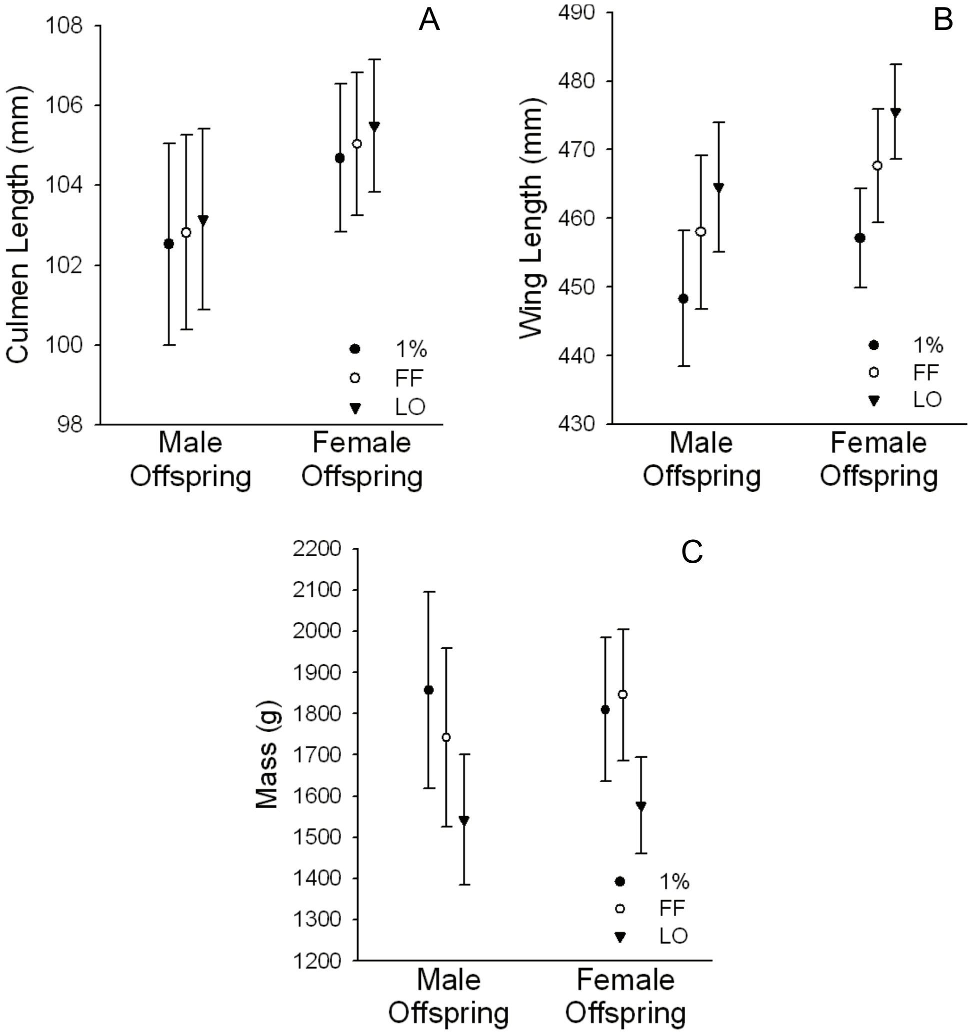

FIG. 1. Comparison of changes in morphological measurements (A: culmen length; B: wing length; C: body mass) between developmental milestones for male and female offspring. Brackets show 95% confidence interval. "1%" indicates the 1% down stage, "FF" = first flight to sea, and "LO" = last observation of the offspring in the colony.

a version of AIC incorporating adjustment of the variance inflation factor, based on an estimate of median c (White 2002). Models with the lowest QAICc values were assumed to better explain variation in the data. Male and female parents were examined in separate analyses because the data independence assumption was violated.

Changes in offspring size between developmental stages were assessed with a repeated measures ANOVA modeled with the morphological measure as the within

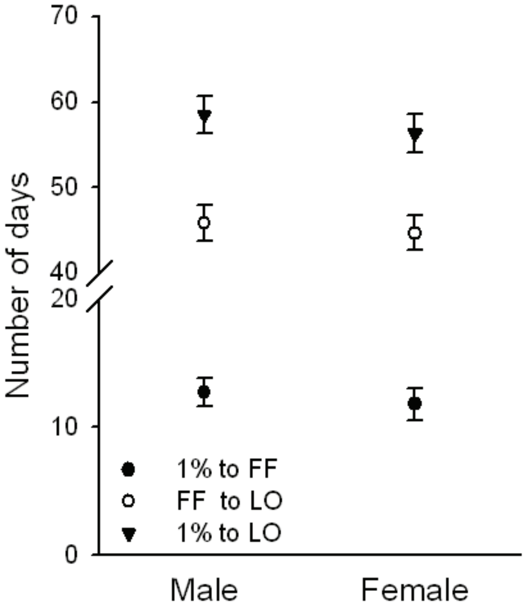

FIG. 2. Number of days between developmental stages of male and female offspring. Brackets show 95% confidence interval. Labels as in Fig. 1.

subject test and offspring sex as the between subjects test. Repeated measures ANOVAs and ANCOVAs were performed in PASW (version 18, SPSS Inc. Somers, NY) all other statistical analyses were performed in Statistica (version 6.1, StatSoft, Inc. Tulsa, OK) unless otherwise noted.

## RESULTS

Eighteen young birds died in 1998–99 after reaching the 1% down stage and 12 died in 2001–02. The sex ratio (proportion of males in the population) of the young that died was 0.50 (95% CI = 0.23–0.77) in 1998–99, 0.75 (95% CI = 0.46–0.91) in 2001–02, and 0.64 (95% CI = 0.43–0.80) for the years combined. Female offspring were not more likely to die during this period than were male offspring in these two years with contrasting sex ratios at the 1% down stage.

*Morphological measurements*. Each offspring was measured approximately four days (95% CI = 2.8–6.0 days) before taking its first flight to sea and again five days (95% CI = 2.2–7.4 days) before departing the colony. Culmen growth increased between developmental stages in both sexes ($F_{(2,17)} = 10.45$, $P = 0.001$) and the amount of growth did not differ between offspring sexes ($F_{(2,17)} = 0.17$, $P = 0.84$). Within subject contrasts revealed that culmen length increased significantly between the 1% down stage and first flight ($F_{(1,18)} = 7.28$, $P = 0.015$) and marginally increased between first flight and last observation ($F_{(1,18)} = 3.93$, $P = 0.063$; Fig. 1A). Wing length also increased between developmental stages in both sexes ($F_{(2,17)} = 39.54$, $P < 0.001$) and the amount of growth did not differ between offspring sexes ($F_{(2,17)} = 0.16$, $P = 0.86$). Within-subject contrasts revealed that wing length increased significantly between the 1% down stage and first flight ($F_{(1,18)} = 36.96$, $P <$

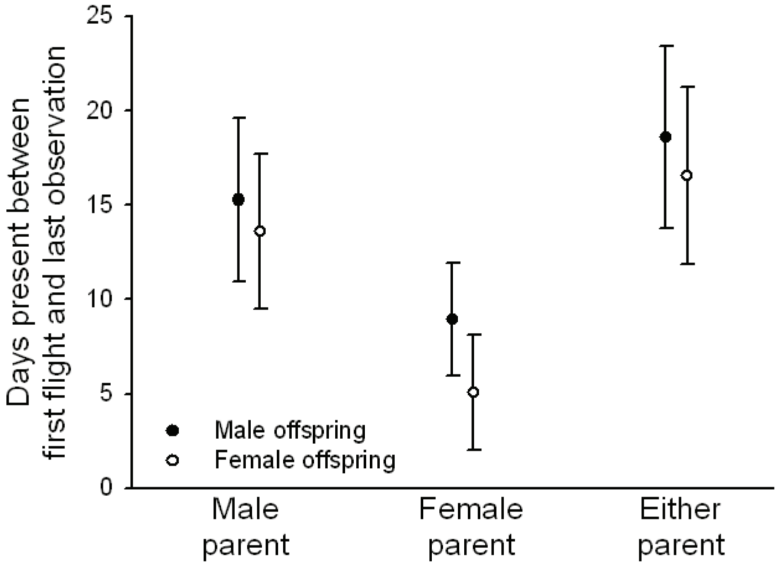

FIG. 3. Proportion of days parents are observed at nest sites during the post-fledging parental care period. Brackets indicate 95% confidence limits.

0.001) and between first flight and last observation ($F_{(1,18)}$ = 19.13, $P < 0.001$; Fig. 1B). Body mass changed significantly between developmental stages ($F_{(2,17)}$ = 9.99, $P$ = 0.001), but changes did not differ between offspring sexes ($F_{(2,17)}$ = 0.49, $P$ = 0.62). Body mass did not change between the 1% down stage and first flight in either sex ($F_{(1,18)}$ = 0.281, $P$ = 0.60), but decreased significantly between first flight and last observation in both sexes ($F_{(1,18)}$ = 12.80, $P$ = 0.002; Fig. 1C).

*Offspring's developmental schedule.* The numbers of days between the 1% down stage and first flight, between first flight and last observation, and between the 1% down stage and last observation did not differ by year, and years were combined for further analyses. None of the durations of these periods differed by offspring sex (Fig. 2). Offspring (sexes combined) flew to sea for the first time 12.3 ± 5.4 (SD) days after attaining juvenile plumage, and vacated the colony 45.3 ± 10.0 (SD) days after first flight and 57.5 ± 10.6 (SD) days after attaining juvenile plumage.

*Parent colony attendance.* The numbers of days that fathers and one or both parents were seen at nest sites between first flight and last observation did not differ by offspring sex (Fig. 3; $F_{(1,30)}$ = 0.36, $P$ = 0.55). The effect of offspring sex on maternal attendance was marginal with mothers of male offspring being present marginally more than were mothers of daughters (Fig. 3; $F_{(1,30)}$ = 3.32, $P$ = 0.08). Fathers were seen at nest sites more often than mothers were during the post-fledging period regardless of offspring sex (Fig. 3; $F_{(1,14)}$ = 6.44, $P$ = 0.024 for male offspring and $F_{(1,14)}$ = 19.47, $P$ = 0.001 for female offspring).

The best models for paternal and maternal nest attendance probabilities were much more supported than the next best model and did not include an effect of offspring sex, but did include an effect of time (Table 2).

Table 2. QAICc rankings of models developed in Program MARK. Survival probability (S) was constrained to be constant (= 1) because all parents survived the two week period examined. Recapture probabilities (p) were modeled as constant (.) or were allowed to vary as a function of sex, or time (t; day), or by incorporating interactions (*) of these factors.

| Model | QAICc | QAICc | QAICc weights | Maximum likelihood | Number of parameters | QDeviance | -2log(L) |
|---|---|---|---|---|---|---|---|
| Fathers | | | | | | | |
| S(.) p(t) | 662.3 | 0.0 | 1 | 1 | 16 | 398.6 | 713.0 |
| S(.) p(sex*t) | 689.6 | 27.3 | 0 | 0 | 32 | 385.6 | 698.2 |
| S(.) p(.) | 710.4 | 48.1 | 0 | 0 | 1 | 479.3 | 804.7 |
| S(.) p(sex) | 711.0 | 48.8 | 0 | 0 | 2 | 477.9 | 803.1 |
| Mothers | | | | | | | |
| S(.) p(t) | 420.6 | 0.0 | 1 | 1 | 16 | 221.1 | 464.6 |
| S(.) p(sex*t) | 446.3 | 25.7 | 0 | 0 | 32 | 199.9 | 439.0 |
| S(.) p(.) | 460.0 | 39.5 | 0 | 0 | 1 | 292.8 | 551.2 |
| S(.) p(sex) | 462.3 | 41.7 | 0 | 0 | 2 | 297.1 | 556.4 |

Median c values for male and female models were 1.136 and 1.209, respectively, indicating minor overdispersion in the global models (White 2002). Both mothers and fathers were more likely to be present at their nest sites after their offspring were last observed than they were before (Fig. 4). Parents were less likely to be present in the days immediately preceding and on the day their offspring vacated the colony than they were at any other time during the two weeks surrounding offspring departure (Fig. 4). Few parents were present in the colony on the day that their offspring vacated the colony, and fathers and mothers were seen more often at their nest site during the week after their offspring's final departure than they were during the previous week (Fig. 4; fathers: $z = 2.24$, $P = 0.025$; mothers: $z = 3.82$, $P < 0.0001$).

## DISCUSSION

Young Nazca Boobies vacate the natal colony at Punta Cevallos one to two months after fledging, and the duration of this period did not differ by offspring sex (Fig. 2). The proportion of days parents of volant young spent at their nest site also did not differ by offspring sex (Fig. 3). We did not measure food delivery to offspring in this study because visual observations of regurgitations are likely to be uninformative (Anderson & Ricklefs 1992) and frequent weighings to detect mass increments (Anderson & Ricklefs 1992) are not possible due to spotty attendance by the fledglings. It is possible that one offspring sex received more food during this period, but this was not reflected by morphological measurements, mortality likelihood after the 1% down stage, the duration of post-fledging care period, or by the parent's attendance. Mothers of female offspring attended their nest sites marginally less than mothers of male offspring, which could indicate that female offspring received less care than male offspring did during this period. Male and female offspring lost similar amounts of body mass after fledging; however, females are structurally larger than males (Fig. 1; Nelson 1978, Townsend *et al.* 2007) and vacated the colony at the same body mass as males (Fig. 1). This result suggests that females vacate the

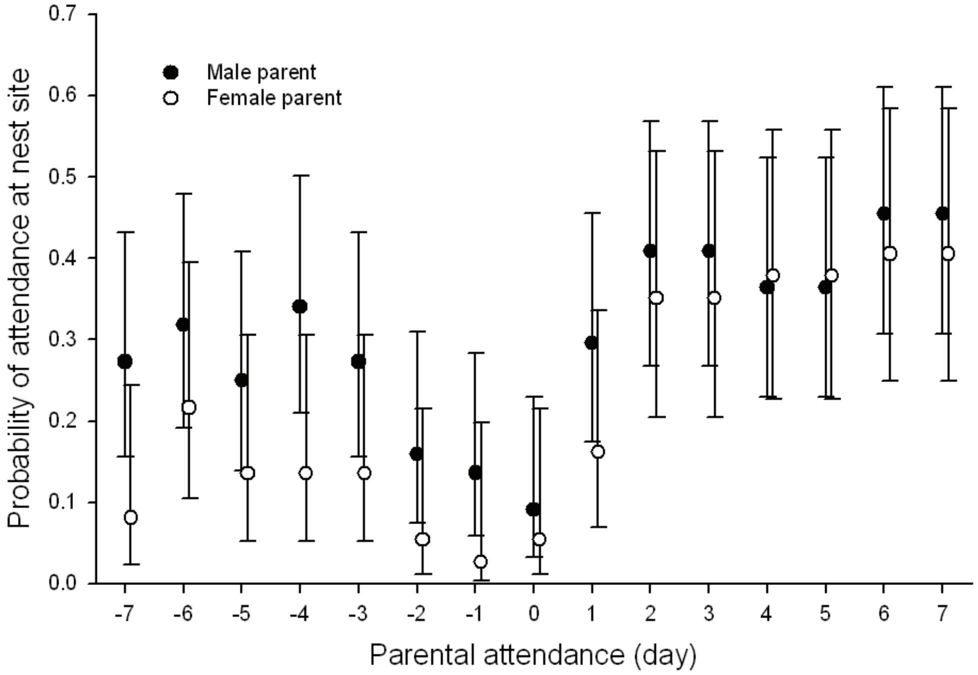

FIG. 4. Probability of parents attending their nest site during the week before and the week after their offspring vacated the colony. Departure date was standardized for comparison; day 0 is the last day that a given offspring was observed in the colony. Brackets indicate 95% confidence limits.

colony in poorer condition than males do, and this difference probably contributes to the higher mortality rate in females than males during the juvenile period at sea (Maness *et al.* 2007).

Our results give no indication that male and female offspring induce different costs for parents after the 1% stage. Our study is the first to compare sex-specific parental care to male vs female offspring during this period in a sulid (Table 1), despite the fact that most species are sexually size dimorphic (Nelson 1978) and that offspring are likely to have different food requirements (Townsend *et al.* 2007). The post-fledging period is of intermediate duration in this species compared to other sulids (Table 1).

Post-fledging Nazca Boobies were seen begging and parents were observed feeding their young until the offspring vacated the colony (pers. observ., see also Nelson 1978). Our data suggest that parental care did not continue after fledglings were seen for the last time. Most parents were not present on the day that their offspring departed the colony, or the day before, and male and female parents attended their nest sites more often after their young departed than they did prior to departure (Fig. 4). Nazca booby parents feed their young by regurgitation, and feeding a juvenile at sea would be difficult. We are not aware of any observation of a sulid feeding an offspring on the water. Band recoveries indicate that juveniles live at sea, north of Galápagos and west of Central America, during their first several years of independence (Huyvaert & Anderson 2004). Since parents and their offspring did not leave the colony together, and parents resided in the colony after their offspring's departure, parents probably cannot locate and care for their young away from the island. The marked absence of parents on the day of, and the two days prior to, their offspring's departure from the island (Fig. 4) leads us to speculate that parents surveyed the nest site around the time of their offspring's departure to avoid visiting while their offspring was present, and that offspring may have used the absence of both parents as part of the "decision" to depart. Recent work on Red-footed Boobies (*Sula sula*) suggests that parents force offspring to become independent by reducing the amount of food they deliver to their offspring (Guo *et al.* 2010). This prediction, which was proposed by Arroyo *et al.* (2002), is supported by our results.

Male parents attended their nest sites more often than female parents did, regardless of offspring sex (Fig. 3). These males may have been guarding their nest site territories from potential rivals (Maness & Anderson 2008) and/or attending to their offspring more than their mates did. Alternatively, female parents may have been foraging more for their offspring than their mates did during this period, especially for their daughters (Apanius *et al.* 2008). Thus, it is difficult to ascertain if one or the other parent invested more effort in offspring care during the post-fledging period.

As a whole, our results are consistent with similar parental care for male and female offspring after they attain juvenile plumage in the two breeding seasons studied, despite the fact that young females are larger and heavier than young males are and appear to require more parental care than sons do to reach the same level of condition (Townsend *et al.* 2007, Apanius *et al.* 2008). Associated with the lack of extra care for daughters, female offspring are more likely to show a prolonged period of dependence on parents and poor growth than are male offspring in Nazca Boobies (unpubl. data), and mortality of juvenile females exceeds that of juvenile males between fledging and their return to the island as adults (Maness *et al.* 2007). This poor performance of young females, and their associated mortality risk, leads to the male bias found in the adult sex ratio of this population (Maness *et al.* 2007).

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